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Performance of *Cotesia flavipes* (Hymenoptera: Braconidae) in parasitizing *Chilo partellus* (Lepidoptera: Crambidae) as affected by temperature and host stage

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Abstract

The braconid larval parasitoid, *Cotesia flavipes*, is used as a biological control agent against the crambid *Chilo partellus*, a serious pest of cereal crops in eastern and southern Africa. We examined the survival, development parameters, and body growth patterns of the host and its parasitoid at different temperatures (22, 26, and 30 °C) using third and fourth instars of *Ch. partellus*. For non-parasitized hosts, larval mortality tended to be highest at lowest temperature and for parasitized at third host instars only at highest temperature. Development time of *Co. flavipes* immatures significantly decreased with host instar and with temperature. Sex ratio of *Co. flavipes* varied from male- to female-biased with increase in temperature. The increase in body weight of parasitized fourth instar *Ch. partellus* was higher than in non-parasitized larvae at all temperatures. Parasitism by *Co. flavipes* had no effect on the food uptake by *Ch. partellus*, but significantly less food was consumed by both parasitized and non-parasitized larvae at 26 °C. The results of this study were discussed in light of the performance of *Co. flavipes* under different climatic conditions.

Keywords: *Cotesia flavipes*; *Chilo partellus*; Parasitism; Temperature; Host stage; Growth patterns

1. Introduction

The crambid *Chilo partellus* is an exotic stemborer species accidentally introduced in East Africa sometime before the 1930s (Harris, 1990). *Ch. partellus* has colonized new areas and its pest status is gradually increasing in Africa. Cereal crops are infested from early whorl stage and losses induced by larvae of *Ch. partellus* in maize in East Africa can cause up to 40% yield reduction (Seshu Reddy, 1998). *Ch. partellus* is progressively replacing native lepidopteran stemborer species and is becoming the predominant stemborer in many areas, especially at low elevation (below 1500 m), but the pest is also expanding its distribution to higher elevation (Kfir, 1997; Overholt et al., 2000; Zhou et al., 2001).

Cotesia flavipes is a gregarious, larval endoparasitoid of lepidopteran stemborers that infest cereal crops. This braconid has been successfully introduced into more than 40 countries as part of the tropics and subtropics in classical and new association biological control programs of crambid stemborers, primarily those in the genera *Chilo* and *Diatraea* (Polaszek and Walker, 1991). In East Africa, *Co. flavipes* is used as a classical biological control agent of *Ch. partellus* (Overholt et al., 1997). *Co. flavipes* populations are gradually increasing in Kenya, northern Tanzania, and Uganda, and the parasitoid is currently being released in many more countries in eastern and southern Africa.

As *Co. flavipes* is a koinobiont, host larvae continue to feed and damage infested plants after being parasitized. Parasitoid development within the host is affected by both environmental factors such as temperature (Mendel et al., 1987) and factors depending on the host itself such as host stage and quality (Tillman et al., 1993).

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Several studies have evaluated the effects of temperature on the developmental time and mortality of both *Ch. partellus* (Berger, 1989; Mbapila and Overholt, 2001) and *Co. flavipes* (Ngi-Song et al., 1995; Omwega and Overholt, 1997; Potting et al., 1997). Maize tissue consumption and subsequent maize yield losses induced by *Ch. partellus* were investigated by Ofomata et al. (2000) and Songa et al. (2001). Hailemichael (1998) studied the growth patterns of African stemborers after being parasitized by *Cotesia* spp. However, no information exists on the influence of parasitism by *Co. flavipes* on the life history, food uptake, and efficiency of food conversion into body mass of *Ch. partellus* host larvae.

Although *Co. flavipes* has dramatically reduced populations of stemborers in East Africa, its impact and rate of parasitism varied from one agro-ecological zone to another (Kfir et al., 2002). The reasons for this are largely unknown but temperature is mentioned as one of the major factors responsible for the variability in the performance of the parasitoid. In the present study we evaluated growth and development of *Co. flavipes* parasitizing *Ch. partellus* as affected by temperature and host stages.

2. Materials and methods

2.1. Host plant

The maize variety Hb511 was planted at the International Center of Insect Physiology and Ecology (ICIPE) experimental station in Duduville, Kenya. Plants were rain-fed and fertilized with NPK 14-10-10 at the rate of 200 kg/ha, 2 weeks after planting. Pieces of fresh maize stem (≈5 cm long) were collected from 6- to 10-week-old plants and soaked for 5 min in a 0.35% solution of sodium hypochlorite for disinfection. The stem pieces were then rinsed twice in distilled water and air-dried on sterile tissue paper in the laboratory before being infested with pre-weighed *Ch. partellus* larvae.

2.2. Insects

Cultures of *Ch. partellus* larvae and the parasitoid *Co. flavipes* were obtained from a laboratory colony established at ICIPE. The colony of *Ch. partellus* and *Co. flavipes* originated from field-collected individuals from the coastal region of Kenya in 1998 and northern Pakistan in 1991, respectively. However, feral individuals are added to the colonies twice a year to maintain genetic diversity. Larvae of *Ch. partellus* were reared on an artificial diet (Ochieng et al., 1985) at 25 °C with a 50–80% relative humidity and a 12L:12D photoperiod. The *Co. flavipes* colony was maintained using *Ch. partellus* larvae as hosts according to methods described by Overholt et al. (1994).

2.3. Experimental protocol

For the experiments, two different host stages, third and fourth instars (L3 and L4), of *Ch. partellus* were used both in non- and parasitized larval treatments. Larvae of *Ch. partellus* at the appropriate stages were removed from artificial diet and fed for 24 h on pieces of maize stem for acclimatization before the start of the experiment. For the parasitized treatment, *Ch. partellus* larvae were exposed to 24-h-old mated *Co. flavipes* females for oviposition using the hand-stinging method; only one stinging was allowed per larva and adult parasitoid. Parasitized and non-parasitized *Ch. partellus* larvae were thereafter placed individually in a glass vial containing a maize stem piece, and plugged with cotton. The vials were kept in incubators at 22, 26, and 30 °C, at 40–65% relative humidity, and at a 12L: 12D photoperiod. Mean temperatures in the major maize growing areas of Kenya ranged from 22 to 31 °C (Jaetzold and Schmidt, 1982).

For each host stage and temperature 120 larvae were parasitized. Of each parasitized group 60 larvae were dissected to measure larval parasitoid weight using a microbalance (Mettler AE166, Mettler Toledo, Switzerland). Various host growth and development parameters were recorded using the remaining 60 parasitized larvae. For the non-parasitized treatment, only 30 *Ch. partellus* larvae were used per host stage and temperature to assess the host larval growth and development parameters, as host mortality was expected to be substantially lower than in the parasitized treatment. The stem pieces were changed every 2–3 days.

2.3.1. Survivorship and body mass growth of Ch. partellus

Survivorship of *Ch. partellus* larvae exposed to *Co. flavipes* and percent pupation in the non-parasitized group were noted any time the food was changed. In addition, larval weight was recorded to the 0.1 mg. In case a parasitized host pupated in the course of the experiment, this individual was excluded from the analysis.

2.3.2. Food uptake by Ch. partellus and its conversion efficiency

To measure the food uptake, consumed stem pieces without frass were weighed. To account for evaporation, 30 glass vials containing a 5 cm non-infested pieces of pre-weighed maize stems each, were kept at 22, 26, and 30 °C, respectively. The stem pieces were weighed at the time the larval food was changed, and total evaporation was calculated as the difference between the initial weight and the final weight. The amount of food consumed was calculated as the difference between stem weight at the time of infestation and the weight when it was replaced, minus the mean evaporation for the corresponding temperature. Food conversion efficiency

by *Ch. partellus* larvae was estimated by dividing the weight gain during a period by the food uptake of that period.

2.3.3. Progeny production, immature development, and larval weight of Co. flavipes

Number of *Co. flavipes* cocoons and adults obtained per successfully parasitized larva were recorded. The time until cocoon formation from the date larvae were stung was recorded for each larva. In case a stung host remained in the larval stage 2 weeks after 50% of larvae had pupated or produced parasitoid cocoons, this larva was dissected to determine if any parasitoid encapsulation by host hemocytes had occurred.

Five parasitized *Ch. partellus* from the group kept for monitoring growth and development of *Co. flavipes* immatures were dissected per temperature treatment and host stage. The dissection was conducted daily starting from 9 and 6 days after parasitization for L3 and L4, respectively. Parasitoid larvae were removed from the host and placed onto a pre-weighed aluminum tray. The parasitoid larvae from each *Ch. partellus* host larva were air-dried for 1 h in the laboratory before being weighed to the nearest 0.1 mg. The number of *Co. flavipes* immature within each host was also counted and recorded. Mean weight of *Co. flavipes* larva was calculated by dividing the weight of the group by the number of individuals within the group.

2.3.4. Potential growth index of Co. flavipes

The potential growth index of *Co. flavipes* for each host stage and temperature treatment was computed as the product of the percentage of stung larvae producing adult progeny, the mean number of adults progeny emerged per host larva, and the sex ratio (proportion of females), divided by the immature period of the parasitoid, i.e., the egg to adult emergence development time (Sétamou et al., 1999).

2.4. Data analysis

Homogeneity of the survival curves of the two larval stages of *Ch. partellus* subjected to different temperatures and parasitism regimes was examined with the likelihood ratio using the LIFETEST procedure of SAS (SAS, 1996). The percentage of host acceptability and suitability was analyzed by a log-likelihood test using a two- and three-dimensional contingency table (Zar, 1999). A factorial analysis of variance was used to examine the effect of host stage and temperature on the immature developmental times and numbers of *Co. flavipes* per host larva. Where significant F values were obtained, treatment means were separated using the Student–Newman–Keuls test (Zar, 1999). The growth of body mass accumulation in non- and parasitized *Ch. partellus* was assessed by a mixed model ANOVA.

3. Results

3.1. Survivorship and fate of Ch. partellus after parasitism by Co. flavipes

Survivorship of parasitized *Ch. partellus* larvae varied significantly with host stage ($\chi^2 = 15.32$; $df = 1$; $P < 0.0001$; Figs. 1B and D), with L3 exhibiting a lower survivorship compared to L4. There was no significant difference between the survivorships of non-parasitized L3 and L4 ($\chi^2 = 2.04$; $df = 1$; $P = 0.15$; Figs. 1A and C). The temperature by host stage interaction was significant only for parasitized larvae ($\chi^2 = 8.25$; $df = 2$; $P = 0.004$; Figs. 1C and D); the survivorship of parasitized L3 larvae increased with higher temperature (Fig. 1B) while no temperature effect was observed on that of parasitized L4 larvae (Fig. 1D). Similarly, the interaction of parasitism and temperature was significant for L4 only ($\chi^2 = 12.50$; $df = 2$; $P = 0.0004$; Figs. 1C and D). No significant differences were observed between the survivorships of non-parasitized L3 ($\chi^2 = 1.55$; $df = 2$; $P = 0.46$; Fig. 1A) and parasitized L4 larvae ($\chi^2 = 0.17$; $df = 2$; $P = 0.92$; Fig. 1D) at different temperatures.

Analysis of three-dimensional contingency table showed that the proportion of successfully parasitized *Ch. partellus* larvae by *Ch. partellus* was independent of temperature and host stage ($\chi^2 = 12.35$; $df = 7$; $0.1 < P < 0.25$; Table 1), whereas the proportion of encapsulated larvae was significantly affected by temperature and by host stage ($\chi^2 = 16.41$; $df = 7$; $0.025 < P < 0.05$). Encapsulation of *Co. flavipes* by the hymocytes of L3 *Ch. partellus* was not different at the three tested temperatures, but for L4 larvae, the rate of encapsulation was significantly higher at 30 °C (Table 1).

3.2. Body mass accumulation, food uptake, and conversion efficiency by Ch. partellus

The growth pattern of *Ch. partellus* larvae is shown in Fig. 2. At all temperatures, parasitism had no significant effect on body mass accumulation of L3 ($F = 0.01$; $df = 1$, 118; $P = 0.92$; Fig. 2). Parasitized L4 larvae grew faster than non-parasitized almost during the entire larval period at all temperature especially at 26 °C (Fig. 2B) and 30 °C (Fig. 2C) ($F = 75.96$; $df = 1$, 141; $P < 0.0001$).

Mean (±SE) evaporation of maize stems were 0.108 (±0.002), 0.170 (±0.015), and 0.246 (±0.005) g/day at 22, 26, and 30 °C, respectively. Accumulated food consumption by parasitized and non-parasitized *Ch. partellus* larvae is shown in Fig. 3. The total food consumption significantly varied with temperature for both L3 ($F = 102.28$; $df = 2$, 118; $P = 0.0001$; Fig. 3A) and L4 ($F = 7.09$; $df = 2$, 141; $P = 0.002$; Fig. 3B), with L3 consuming significantly more food at 30 °C than at 22 and 26 °C. Both L3 and L4 larvae had the lowest food uptake at 26 °C. Total food consumption of parasitized L4 was

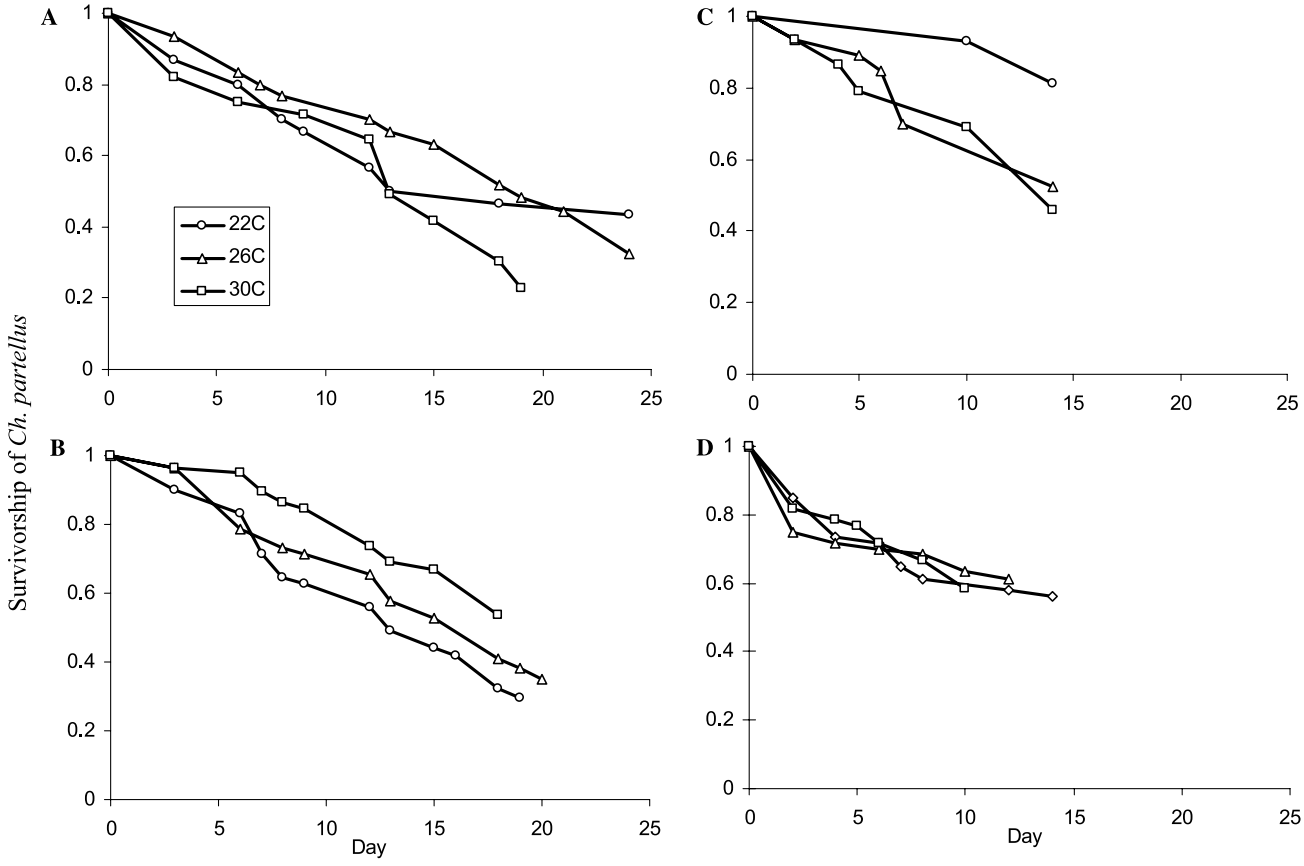

Fig. 1. Survivorship of third (L3) and fourth (L4) instars *Chilo partellus* larvae as affected by temperature and parasitism by *Cotesia flavipes*. (A) Non-parasitized L3, (B) parasitized L3, (C) non-parasitized L4 larvae, and (D) parasitized L4.

Table 1
Fate of third and fourth instar *Chilo partellus* larvae parasitized by *Cotesia flavipes*, and percentage of adult parasitoids emerged from cocoons at different temperatures

Host stage	Temperature (°C)	*N*	% Hosts forming cocoons	% Hosts forming pupae	% Hosts encapsulated	% Adult emerged
L3	22	59	20.34a	0.00a	13.56a	40.00b
	26	49	24.49a	0.00a	16.67a	75.00a
	30	48	22.92a	0.00a	18.37a	83.33a
L4	22	57	40.35a	12.28a	1.75b	87.50a
	26	56	41.07a	16.07a	1.79b	95.65a
	30	55	23.64a	14.54a	16.36a	92.31a

N represents the initial number of host larvae stung in each treatment. Means within the same column followed by different letters are significantly different ($P < 0.05$, Student–Newman–Keuls' test).

comparable to that of non-parasitized L4 at all three tested temperatures (Fig. 3B). In contrast, at 30 °C, parasitized L3 consumed significantly less food than non-parasitized L3 larvae ($F = 10.04$; $df = 1, 38$; $P = 0.0026$; Fig. 3A), but no significant differences were detected at 22 and 26 °C. Mean total food consumptions of 0.5 g at 22 °C and of 1.2 g at 26 °C for L3 larvae were lower than the mean total food uptake of 0.9 and 1.6 g for L4 at 22 and 26 °C, respectively (Figs. 3A and B).

The food conversion efficiency decreased with time in all treatments, from ≈0.02 and 0.04 for L3 and L4, respectively, to 0 at the time of pupation or parasitoid emergence (Fig. 4). Parasitized L4 larvae were more efficient during the first 8–10 days at 22 °C (Fig. 4A) and 26 °C (Fig. 4B) than non-parasitized L4 larvae. There was no significant difference between parasitized and non-parasitized L3 for the food conversion rates at all temperatures (Fig. 4).

3.3. *Co. flavipes* progeny production, immature development, and potential growth index

The developmental time of *Co. flavipes* immatures within L4 *Ch. partellus* was inversely related to temperature ($F = 15.28$; $df = 2, 56$; $P < 0.0001$; Table 2). Cocoon developmental time was much longer at all temperatures

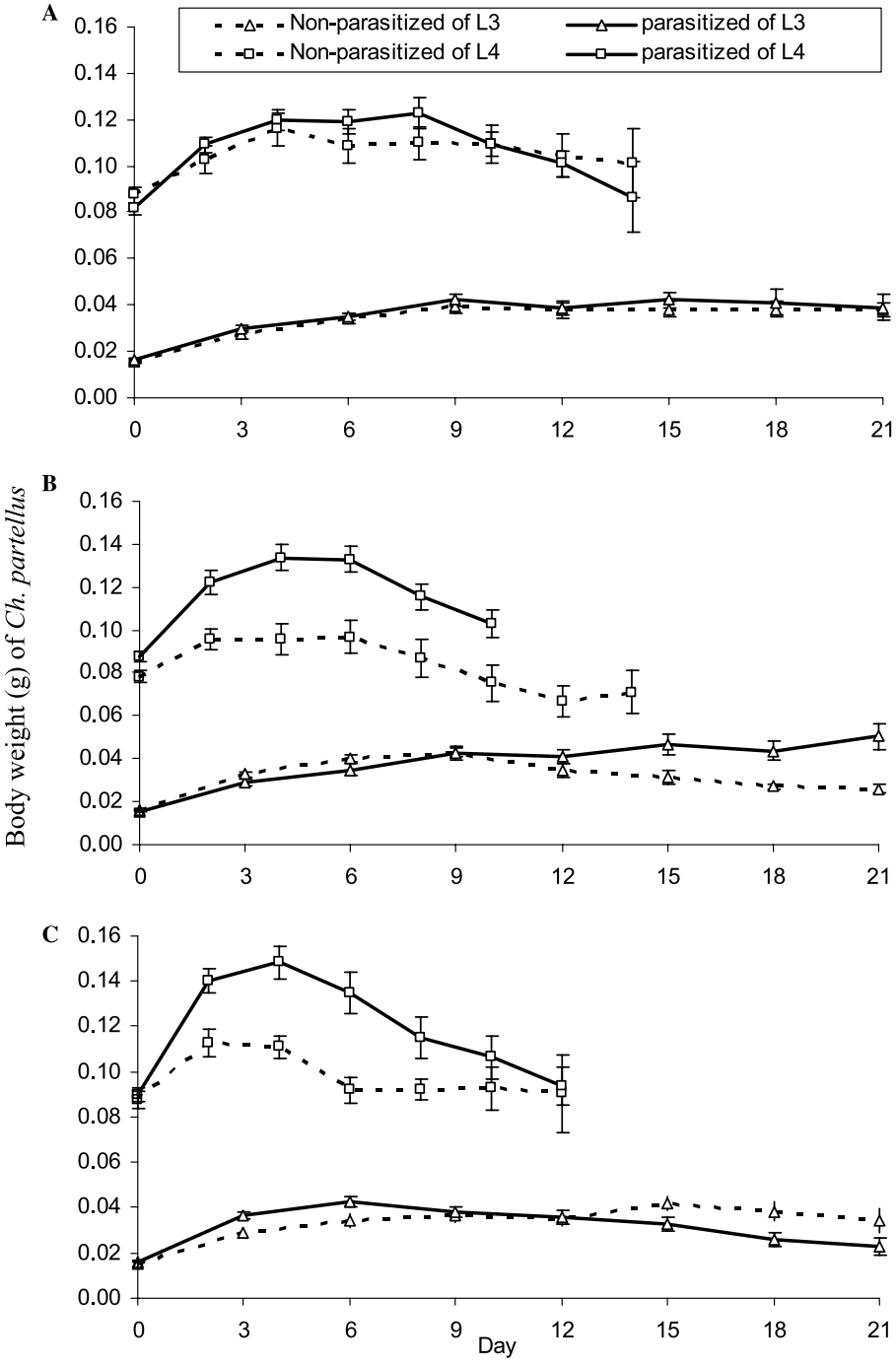

Fig. 2. Body mass (±SE) growth of successfully parasitized L3 and L4 *Chilo partellus* at different temperatures, i.e., 22 °C (A), 26 °C (B), and 30 °C (C).

when L3 was used as the host compared to L4 ($F = 91.69$; $df = 1, 89$; $P < 0.0001$; Table 2).

Significantly more parasitoids emerged when *Ch. partellus* L4 was the host than L3 ($F = 18.84$; $df = 1, 89$; $P < 0.0001$; Table 2). Similarly, the number of *Co. flavipes* adults emerged per larva increased with temperature for L4 only ($F = 3.98$; $df = 2, 56$; $P = 0.025$; Table 2), but not for L3 ($F = 1.96$; $df = 2, 32$; $P = 0.1643$). *Co. flavipes* progeny sex ratio was affected by temperature; sex ratio was female-biased at 30 °C, whereas more males emerged at lower temperatures on both L3 ($F = 7.41$; $df = 2, 32$; $P = 0.0035$; Table 2) and L4 ($F = 17.42$; $df = 2, 56$; $P < 0.0001$). However, there was no effect of host stage on progeny sex ratio ($F = 0.18$; $df = 1, 89$; $P = 0.67$). The sample size of *Co. flavipes* adults emerging from L3 host at 26 °C was too small to allow any reliable statistical inference of its sex ratio (Table 2).

Dissection of stung *Ch. partellus* larvae showed that the number of parasitoid larvae within each host varied significantly with temperature for L4 only ($F = 4.21$;

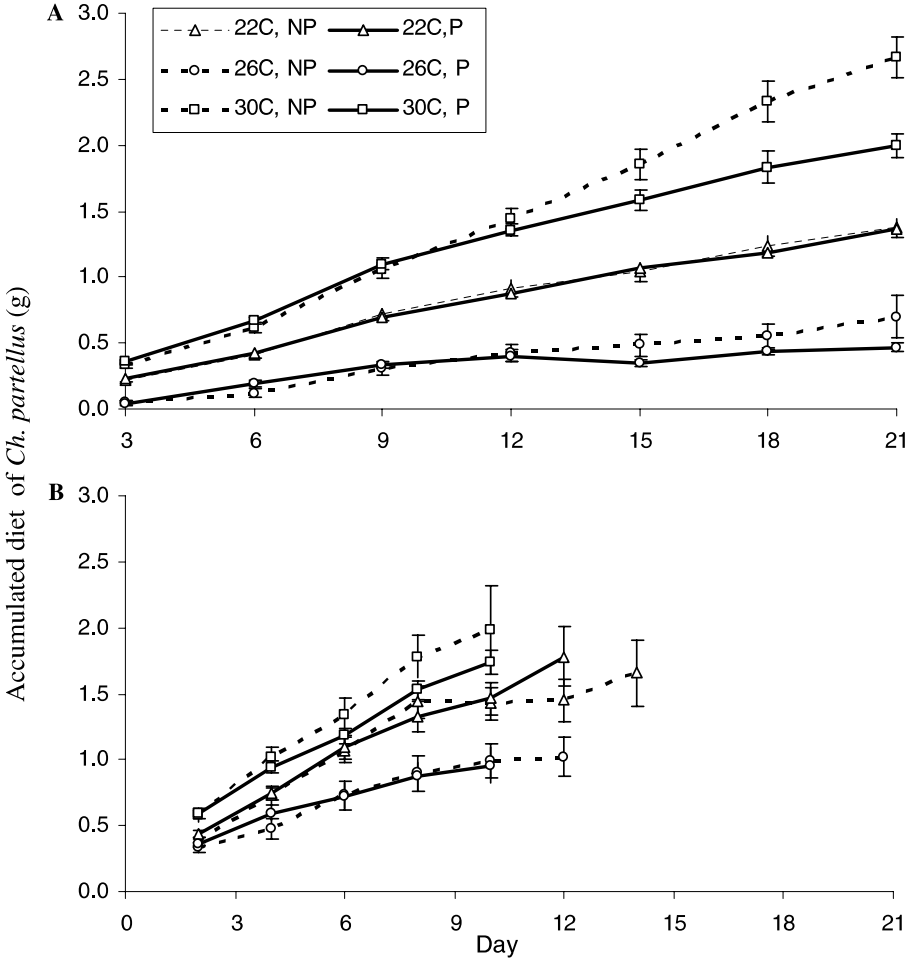

Fig. 3. Accumulated food consumption (±SE) of parasitized (P) and non-parasitized (NP) *Chilo partellus* larvae maintained at three temperatures. (A) L3 larvae, and (B) L4 larvae. Bars represent standard errors of the means.

$df = 2, 56$; $P = 0.02$; Table 3). More parasitoid larvae were recovered from L4 than from L3 at all temperatures tested (Table 3). The body mass of individual *Co. flavipes* larva retrieved per host was not affected by temperature in both L3 ($F = 0.52$; $df = 2, 54$; $P = 0.5960$) and L4 ($F = 2.96$; $df = 2, 56$; $P = 0.06$) (Table 3). The weight of *Co. flavipes* immature recovered from L4 larvae was higher than that of parasitoid immature retrieved from L3 larvae ($F = 106.59$; $df = 1, 112$; $P < 0.0001$; Table 3).

At all temperatures tested, the potential growth index of *Co. flavipes* was higher for the L4 than L3 instars (Table 2). In addition, the index varied with temperature. Parasitized L4 larvae developing at 26 °C yielded the highest growth index.

4. Discussion

Results of the present study indicated that both host stage and rearing temperature are important factors affecting survival, growth, and development parameters of *Co. flavipes*. The rate of development of *Co. flavipes* was inversely related to temperature. These results corroborate findings by Mbapila and Overholt (2001). The parasitoid also requires a shorter time to develop from egg to cocoon in parasitized L4 than in L3. This could indicate a lower rate of development in smaller host due to a lack of adequate food supply (Tauber et al., 1983). Rapid development of parasitoids on small hosts may lead to host death which will be detrimental to the parasitoid as well. Thus, to ensure its development is successfully completed, *Co. flavipes* may regulate the host and adjust its own development rate. In L4, however, the fitness of the parasitoid immature is increased because of a larger food supply, leading to a higher development rate. This increase in parasitoid fitness in L4 might also explain the lower host mortality observed for this host stage compared to L3. These results corroborate findings by Ngi-Song et al. (1995) who observed higher host mortality in younger host stages of *Busseola fusca* Fuller (Lepidoptera: Noctuidae) parasitized by the indigenous braconid *Cotesia sesamiae*. Although Mbapila and Overholt (2001) reported that encapsulation is uncommon

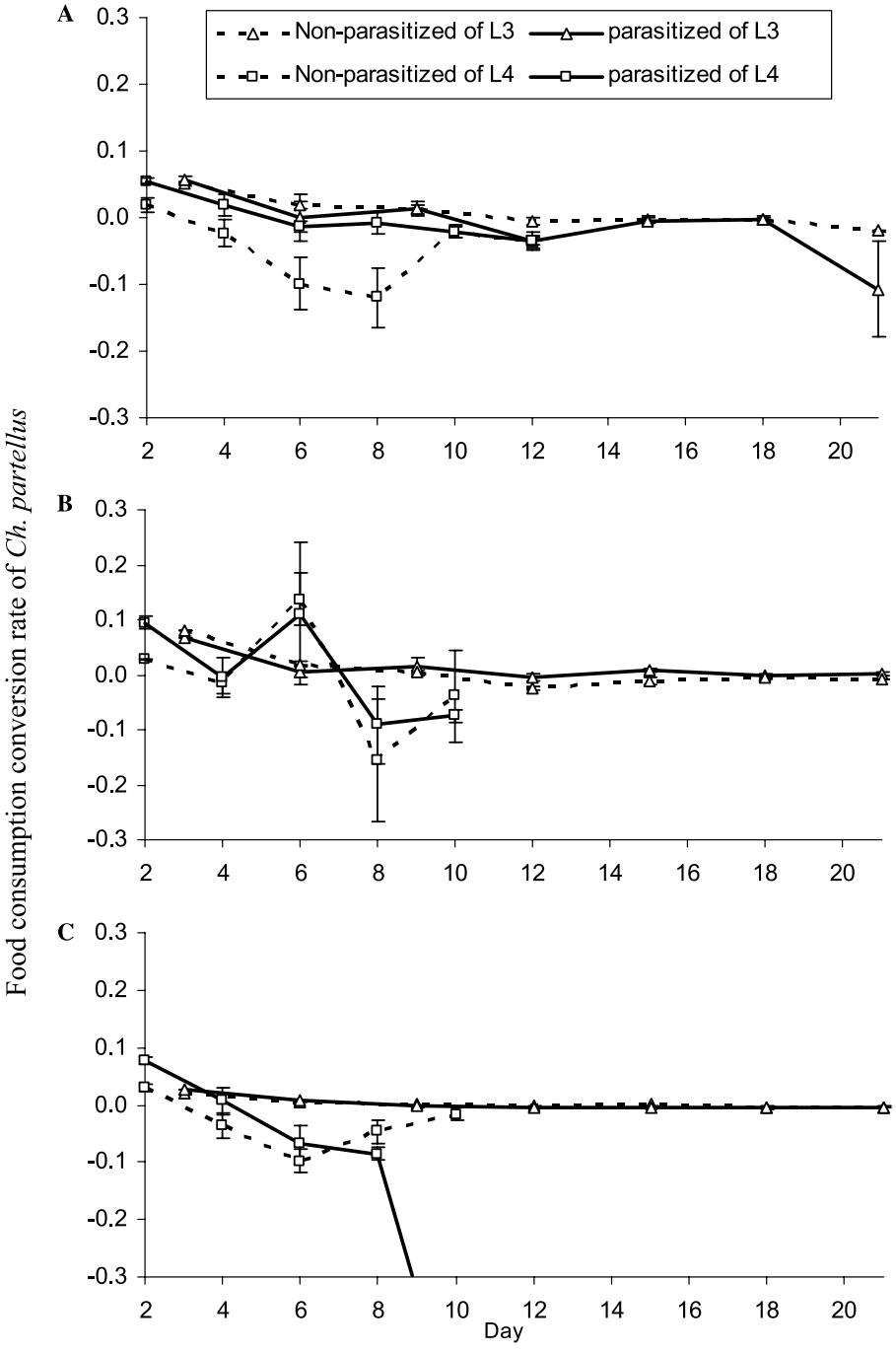

Fig. 4. Mean food conversion rates by parasitized (P) and non-parasitized (NP) L3 and L4 *Chilo partellus* larvae maintained at three temperatures. (A) 22 °C; (B) 26 °C; and (C) 30 °C. Bars represent standard errors of the means.

for *Co. flavipes* parasitizing *Ch. partellus*, the proportion of encapsulated larvae ranged from 2 to 18% in our study. The higher proportion of *Ch. partellus* larvae encapsulating *Co. flavipes* immatures observed at 30 °C for L4 might be due to a faster host development at this temperature, leading to an increase in the host immune response.

More parasitoid larvae were recovered from parasitized L4 than L3 after dissection suggesting that the parasitoid laid significantly more eggs on larger hosts. As a consequence, the number of *Co. flavipes* emerging per larva was significantly higher for L4 than L3. Rearing temperature did not affect the number of parasitoid immatures and adults recorded per host larva. Although the clutch size was not affected by temperature, the sex ratio of the progeny was significantly affected by temperature with more males being produced at 22 °C. Previous studies on L4 larvae did not show any effect of temperatures on progeny sex ratio of *Co. flavipes* (Mbapila and Overholt, 2001; Ngi-Song et al., 1995;

Table 2
Cotesia flavipes developmental time (means ± SE) from egg to cocoon formation, brood size and sex ratio of adults per host larva, and its potential growth index on third and fourth instar *Chilo partellus* maintained at different temperatures

Temperature (°C)	Immature developmental time in days		Brood size per larva		Sex ratio		PGI	
	L3	L4	L3	L4	L3	L4	L3	L4
22	18.60 ± 0.64aA	14.08 ± 0.44aB	6.67 ± 2.09aA	12.05 ± 2.06bA	0.23 ± 0.07bA	0.12 ± 0.03cA	0.03	0.04
26	17.09 ± 0.89aA	11.64 ± 0.18bB	1.67 ± 0.29aB	23.96 ± 3.96aA	0.15 ± 0.11bB	0.42 ± 0.07bA	0.02	0.22
30	17.48 ± 0.89aA	11.82 ± 0.41bB	6.00 ± 2.47aB	25.83 ± 5.64aA	0.70 ± 0.12aA	0.64 ± 0.07aA	0.13	0.15

Means within each column followed by different lower case letters are significantly different ($P = 0.05$, Student–Newman–Keuls' test). For each variable, means across the same row followed by the same capital letter are not significantly different ($P < 0.05$, Student–Newman–Keuls' test).

Table 3
Mean (±SE) number and weight of *Cotesia flavipes* immatures recovered from parasitized third and fourth instar *Chilo partellus* developing at different temperatures

Temperature (°C)	Number of immatures		Weight (in mg) per individual	
	L3	L4	L3	L4
22	23.13 ± 4.51aB	45.50 ± 4.91aA	1.70 ± 0.76aB	11.18 ± 1.11aA
26	13.00 ± 2.66aB	29.50 ± 6.37bA	1.16 ± 0.27aB	10.48 ± 1.98aA
30	17.20 ± 3.31aB	52.93 ± 4.85aA	1.13 ± 0.27aB	17.20 ± 3.17aA

Means within the same column followed by the same lower case letter, and for each variable means across the same row followed by the same capital letter are not significantly different ($P < 0.05$, Student–Newman–Keuls' test).

Potting et al., 1997); however, these studies were conducted at temperature ranging between 25 and 30 °C. Thus, the present results suggest that low temperature could negatively affect the establishment of *Co. flavipes* and its performance in biological control programs. Since *Co. flavipes* females used to sting larvae originated from the stock cultures and maintained under the same climatic conditions, it is most likely that the significant effect of temperature on the progeny sex ratio is due to a differential mortality of male and female immatures within *Ch. partellus*. The male-biased sex ratio coupled with the longer immature development time, will translate into low population growth indices for each subsequent generation. In a 10-year study to assess the impact of *Co. flavipes* in Kenya, Zhou et al. (2003) showed that a 50% reduction in stemborer population occurred in the coastal region where mean ambient temperatures varied from 25 to 26 °C (ACT, 2002), whereas the impact of the parasitoid in cooler climates was minimal. In addition to affecting the development of the parasitoid, low temperature also affects the host development and age–structure composition of *Ch. partellus*. Most likely, younger and smaller host instars are available for a longer period in cooler climates than at higher temperatures.

The suitability of various stemborers for growth and development of *Co. flavipes* has been studied by Ngi-Song et al. (1995), Alleyne and Beckage (1997), Wiedenmann et al. (2003), but no study has been conducted on the host regulation by *Co. flavipes*. In koinobiont species, the parasitoid may manipulate the growth physiology of its host causing premature or delayed maturation at abnormally small or large sizes (Godfray, 1994). Results of the present study clearly indicate that the body mass growth pattern of *Ch. partellus* was affected by parasitism and host instars. In parasitized L3, body mass increased at a slower rate than the non-parasitized L3 larvae, which may be an adaptive response to deficient nutrient conditions (Harvey et al., 1994). Alleyne et al. (1997) also observed that unparasitized larvae of *Manduca sexta* (L.) (Lepidoptera: Sphingidae) grew faster than their counterparts parasitized by *Cotesia congregata* (Say) (Hymenoptera: Braconidae). In contrast, body mass increased faster for parasitized than non-parasitized L4. This is probably due to an acceleration of host maturation, because a full-sized host will contain more resource for parasitoid growth. However, in gregarious species, parasitoid fitness is not only affected by host size but also by the number of parasitoid developing in the host (Alleyne and Beckage, 1997; Charnov and Skinner, 1988; Waage and Godfray, 1985). Parasitized L4 larvae contained more *Co. flavipes* immatures and produced more cocoons than L3, suggesting that either the adult female adjust the number of eggs to be laid to the size of the host, or immature survival of the parasitoid is determined by the host size. In both cases, there is clear indication that *Co. flavipes* regulates the host size for successful completion of its development.

Although parasitism seemed to regulate host growth, it did not influence food consumption in either host stage. At all temperatures except for L3 at 30 °C, parasitized and non-parasitized larvae consumed similar amounts of food. Accumulated food uptake varied significantly with temperature; less food was consumed at 26 °C by either larval stage. The relationship between growth rate of stemborer and its food consumption showed that 26 °C was the optimal temperature, requiring

the least energy for parasitoid and host growth. More food was needed for metabolism at 22 and 30 °C implying more stemborer damage to the plant at those temperatures. Ofomata et al. (2000) reported that a non-parasitized *Ch. partellus* larva consumed ≈5 g of maize tissue during its development from L1 to pupation. In our study, food consumption by non-parasitized larvae was lower than that reported because it did not consider the entire larval period. The results presented here clearly indicate that parasitized and non-parasitized larvae have the same potential for damaging the plant. Thus, the effect of *Co. flavipes* cannot be measured through stemborer damage reduction shortly after parasitoid release, but rather through stemborer population reductions in the following generations in both cultivated and wild habitats. Thus, Zhou et al. (2003) could only detect significant impacts of *Co. flavipes* 5–7 years after releases.

In the context of the performance of *Co. flavipes* in the field, the low food uptake coupled with a high potential growth index of the parasitoid observed at 26 °C, suggest that areas with this ambient temperature would be optimal for *Co. flavipes* performance as shown by the highest potential growth index recorded at this temperature. The characteristics of temperature-dependent development of parasitoids can be useful to conduct and evaluate biological control potential (Miller and Gerth, 1994). Based on results herein reported, releases of *Co. flavipes* should be done in areas with warmer climates (26–30 °C) for successful establishment and sustained reproduction of the parasitoids.

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